



Effect of prism adaptation on thermoregulatory control in humans

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HIGHLIGHTS

- After visuo-motor adaptation to rightward displacing glasses, the participants' hands temperature decreased.
- After adaptation to neutral lenses and left shifting prisms, we found an increase of the temperature of both hands.
- The results suggest a relationships between body spatial representations and homeostatic control.

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ABSTRACT

The physiological regulation of skin temperature can be modulated not only by autonomic brain regions, but also by a network of higher-level cortical areas involved in the maintenance of a coherent representation of the body. In this study we assessed in healthy participants if the sensorimotor changes taking place during motor adaptation to the lateral displacement of the visual scene induced by wearing prismatic lenses (prism adaptation, PA), and the aftereffects, after prisms' removal, on the ability to process spatial coordinates, were associated with skin temperature regulation changes. We found a difference in thermoregulatory control as a function of the direction of the prism-induced displacement of the visual scene, and the subsequent sensorimotor adaptation. After PA to rightward displacing lenses, with leftward aftereffects (the same directional procedure efficaciously used for ameliorating left spatial neglect in right-brain-damaged patients) the hands' temperature decreased. Conversely, after adaptation to neutral lenses, and PA to leftward displacing lenses, with rightward aftereffects, the temperature of both hands increased. These results suggest a lateral asymmetry in the effects of PA on skin temperature regulation, and a relationship between body spatial representations and homeostatic control in humans.

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1. Introduction

The relationship between the sense of body ownership and the physiological regulation of bodily functions has recently drawn the attention of those researchers interested in understanding how the human brain develops, represents, and maintains a bodily "self" [1–3]. In particular, the link between several physiological parameters (heartbeat, temperature regulation, skin conductance responses, pupil dilatation), different aspects of perception (tactile, thermal, proprioception, pain), and bodily consciousness has been investigated both in healthy participants, and in neurologi-

cal patients showing autonomic dysfunctions, or abnormalities in cortical representations of the body, and the space around it [4–11].

One of the most recent approaches to the study of the relationship between brain mechanisms of bodily self-consciousness and the integrity of the body itself, has made use of perceptual illusions in both healthy participants and clinical populations. Within such paradigms, ambiguous multisensory information about the location and the appearance of one's own body (or body parts) has been used, with the purpose of altering the persons' sense of body ownership, and the regulatory control of their physiological functions [3,9,12]. In particular, the Rubber Hand Illusion has been used to test the hypothesis that hand skin temperature can be modulated by disrupting the sense of ownership over that limb. Specifically, when participants begin to perceive that an artificial limb is part of their own body, the temperature of their real hand (the one placed on the same side of the artificial limb) decreases

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[13,14; see also 15]. Importantly, the temperature's drop observed in the real 'disowned' hand is positively correlated with the vividness of the illusion [13]. In a complementary way, the strength of the Rubber Hand Illusion is increased when a real hand is artificially cooled, while warming the hand decreases the strength of the illusion [7]. In other recent studies, the induction of a Full Body Illusion, obtained by immersing participants in a virtual reality environment, was found to be effective in modulating the exteroceptive sensitivity of the palm of the hand to thermal changes [16], and to cause a widespread drop of the participants' skin temperature [17]. Correspondingly, the sight of the reflection of the participant's limb through a mirror, produced a limb-specific increase in skin temperature: this suggests that the vision of the body could result in an enhanced ownership over the seen limb, thus increasing temperature and homeostatic control, in a process opposite (and complementary) to that acting in the Rubber Hand Illusion [18].

Importantly, disorders of bodily awareness and of thermal regulation are correlated in a number of different neurological and psychiatric conditions, such as schizophrenia [19–22], autism [23,24], epilepsy [25,26], neuropathic pain [27], anorexia nervosa, and bulimia [28,29]. The Complex Regional Pain Syndrome (CRPS) is another clinical condition, whose features include a disruption of thermoregulation [8,30,31], and an altered representation of the body in a number of patients [32–39].

Interestingly, both patients affected by CRPS, and right-brain-damaged patients with left spatial neglect (a multi-componential disorder involving the ability to process spatial information contralateral to the side of the lesion, and/or to perform actions in that side of space [40]), share a number of symptoms [33,34,41–48]. In particular, CRPS patients exhibit a neglect-like, space-based, tactile processing deficit [30] (see also [49] for a study showing that also patients with chronic back pain may show spatial neglect-like symptoms under certain conditions of stimulus presentation). Specifically, in a temporal order judgment task, CRPS patients show a prioritization of vibrotactile stimuli presented on the unaffected hand, when arms are kept uncrossed, and a reversed prioritization when they are crossed over the body midline. These results suggest that the information processing deficits in CRPS patients may be related to body-centered (with reference to the patient's body midline) spatial, rather than to somatotopic (based on the somatosensory representation of the body in the primary somatosensory cortex, area S1) reference frames. CRPS patients show also a deficit in hand skin temperature regulation, with a cooling of the affected limb, related to the prioritization effect: the larger is the difference in temperature between the two hands, the earlier vibrotactile stimuli have to be delivered to the affected hand, in order to be perceived simultaneous to those delivered to the unaffected hand [30]. Interestingly, hand temperature of CRPS patients is modulated by manipulating the position of the hands in peri-personal space, namely: placing the unaffected hand in the "affected" side of space (the one where the affected hand is generally placed), in a position that crosses over the body midline, causes a decrement of hand temperature, suggesting a space-based (body-centered), rather than arm-based (somatotopic), modulation of skin temperature [8].

A further similarity between CRPS and neurological disorders of spatial cognition comes from a single case study. van Stralen and colleagues [50] induced the Rubber Hand Illusion (considered as an experimental measure of disownership of the real hand) on both hands of a right brain-damaged patient suffering from left somatoparaphrenia (a neuropsychological disorder, most often brought about by damage to the right cerebral hemisphere, and characterized by a delusion of disownership of left-sided body parts [51]), and recorded hand skin temperature before and after the induction of the illusion. A decrement in temperature after the induction of the illusion was found, but only in the left, disowned,

hand. This result suggests that thermoregulatory control is related to the sense of body ownership, whose disruption may alter thermoregulation.

Visuo-tactile illusions have been so far a main method to investigate the relationships between spatial processing, body ownership, and thermoregulatory control. However, other tools (based on different neurocognitive mechanisms) may prove to be effective in temporarily altering body and peri-personal space representations. In particular, here we used a prism adaptation (PA) procedure in order to study the link between spatial processing and thermoregulation.

In the PA procedure, participants are asked to perform a series of pointing movements to visual targets, while wearing goggles designed to shift the visual scene laterally. Typically, first pointing movements are biased and deviated in the direction of the displacement of the visual scene brought about by the optical prisms (the so-called "direct effect" [52]). This sensorimotor discrepancy between the planned and the actual movement toward the target enhances a correction in subsequent movements, until the target is reached and the sensorimotor discrepancy reduced (adaptation). When prisms are removed, pointing movements are biased toward the opposite side of the prism-induced displacement (aftereffects). The resolution of the sensorimotor discordance induced by optical prisms displacing the visual scene requires a remapping of bodily and space coordinates into a new egocentric spatial frame of reference. The occurrence of sensorimotor aftereffects, that index successful adaptation, is assessed by measuring the egocentric straight ahead, both before (pre-), and after (post-) prismatic exposure. Straight ahead measures are obtained for the visual, the proprioceptive, and the visual-proprioceptive sensorimotor systems. Proprioceptive and visual-proprioceptive aftereffects are shifted in the opposite direction with respect to the displacement of the visual scene induced by exposure to optical prisms, while visual aftereffects are shifted in the same direction of it [52].

PA has been extensively used to investigate both neural plasticity in healthy participants, and the effect of spatial remapping in the rehabilitation of neuropsychological disorders [53–56] (see [57] for a comprehensive review on PA). PA has been used to treat also the symptoms of CRPS patients, achieving a substantial relief of pain, as well as the amelioration of other symptoms [35,58]. Prismatic lenses have been recently used in CRPS patients to test the hypothesis that its thermal manifestations depend on the perceived location of the hand relative to the body midline, rather than to its actual location. Prisms induced a displacement of the perceived position of the affected hand either towards the affected (ipsilateral), or towards the unaffected (contralateral), side of space, in the latter condition, illusorily crossing the body midline. The patients' pathological arm warmed up (with a reduction of the thermoregulatory dysfunction), when visually perceived in the unaffected, contralateral, side of space, and cooled down when perceived in the affected side, in both conditions regardless of its actual physical position [31]. Accordingly, those cortical mechanisms involved in processing the perceived position of the limbs in space, on the basis of visual and proprioceptive information, may also participate in modulating hands' temperature.

As far as the neural basis of the higher-order modulations of thermoregulatory control is concerned, the temporary interference over the activity of the posterior parietal cortices (PPC) by means of rTMS, reduces hand temperature in healthy participants [59]. The PPC, an area involved in the multisensory integration of stimuli in different sensory modalities [60,61], the maintenance of spatial and body representations [61–63], and the planning of goal-directed movements [64–66], might be also part of a network that exerts a top-down modulation on physiological functions related to body

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